MADROÑO, Vol. 56, No. 1, pp. 23–42, 2009

REPRODUCTIVE BIOLOGY OF THE SAN FERNANDO VALLEY SPINEFLOWER, *CHORIZANTHE PARRYI* VAR. *FERNANDINA* (POLYGONACEAE)

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ABSTRACT

In response to conservation concerns, the reproductive biology of the San Fernando Valley Spineflower was investigated, focusing on pollination interactions and seed germination. Pollination by a variety of aerial visitors, as well as autogamy (a facultative selfer, showing about 25% selfing), appear to contribute significantly to fruit/seed set. There was a significant correlation between the numerous different floral visitors (many went uncollected) and the invertebrate fauna in the immediately surrounding coastal sage scrub community indicating that this taxon is visited by a substantial variety of potential pollinators and is probably not pollinator-limited. Although there were many potential pollinators, only six species, including three species of ants, made up the vast majority of visits to the flowers at the two study sites. Many of the invertebrate visitors to the flowers of the San Fernando Valley Spineflower exhibited a high rate of constancy. An overall generalist strategy is suggested. Seed set was high and a germination rate of over 70% occurred without pre-treatment.

Key Words: Ants, *Chorizanthe parryi* var. *fernandina*, floral constancy, generalist pollination strategy, mixed mating, pollination biology, Polygonaceae, San Fernando Valley Spineflower, selfing.

The present study investigated a variety of the factors associated with the reproductive biology of *Chorizanthe parryi* S. Watson var. *fernandina* (S. Watson) Jepson, the San Fernando Valley Spineflower (SFVS), an herbaceous low-growing annual thought to be extinct (Hickman 1993) until its 1999 rediscovery on the Ahmanson Ranch in Ventura County, California. Subsequently, it was found on the Newhall Ranch, 17 mi northeast of the Ahmanson Ranch, in Los Angeles County (California Natural Diversity Database 2001). Although the Ahmanson Ranch and the Newhall Ranch both support large populations of the SFVS, fewer than 20 acres of habitat at the Ahmanson Ranch (Meyer 2003) and no more than 25 acres at the Newhall Ranch are known to support this species (Mary Meyer, personal communication, California Department of Fish and Game). Therefore, a total of not more than 45 acres of habitat currently exist (at least have been discovered) where this species still can be found.

Historically, this taxon is reported to have had a much larger range extending from Lake Elizabeth in Los Angeles County to near Del Mar in San Diego County (Munz and Keck 1959; Glenn Lukos Associates, Inc. 1999; Jones et al. 2002). Currently, it is designated as a List 1B.1 plant (Rare, Threatened, or Endangered in California or Elsewhere; seriously endangered in California) by the California Native Plant Society and is State-listed Endangered (CNPS 2001) and a Federal candidate for similar listing (CNPS 2005). Knowledge of the reproductive biology of a rare plant is often critical to any management plan developed to ensure the long-term survival of that species (Kearns and Inouye 1997). Such studies involve a detailed analysis of all aspects of plant reproductive biology, including the breeding system, pollination interactions, fruit/seed set, dispersal and germination, growth and survival, etc. (Kearns and Inouye 1993).

Following the rediscovery of the SFVS on the Ahmanson Ranch, a series of surveys and directed research activities were undertaken to determine the size and extent of the on-site populations, any off-site occurrences, and factors important to its survival. These initial studies were reported in Sapphos Environmental, Inc. (2001), which also includes a summary of the known information regarding the pollination biology of this plant. On the basis of an apparently abundant seed set and a brief field observation in 1999, C. E. Jones suggested pollinators were probably not limiting the reproduction of this species. The current study was then developed to address systematically the reproductive factors of pollination interactions and germination success.

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FIG. 1. San Fernando Valley Spineflower at the Ahmanson Ranch, Ventura Co., California. Photo by Bob Allen.

Scope of Study

Given the importance of reproductive biology to the survival of endangered plant species (Harper 1979), this study was designed to initiate an information database addressing the reproductive biology of the SFVS. The specific hypotheses examined are as follows:

1) The SFVS is pollinated by a variety of invertebrate pollinators.
2) Seed-set in the SFVS is not pollinator limited.
3) The SFVS has visitors that demonstrate a high degree of constancy.
4) The SFVS is a facultative selfer.
5) SFVS seed germinates readily without special treatment.

Materials and Methods

Plant Species

The SFVS occurs primarily in dry, sandy places within coastal scrub communities at elevations below 350 m (Munz and Keck 1959). Reveal (1989) has described the SFVS as occurring between about 215 and 335 m, a somewhat narrower range than that listed for *C. p.* var. *parryi* (90–350 m).

Stems of the SFVS spread more or less horizontally from the base to form a low, flat-topped, grayish plant 0.2–0.8 (1) dm high and 0.5–4 (6) dm across (Jepson 1925; Reveal 1989; Fig. 1). Leaves are mostly basal, 0.5–2.5 (4) cm long, oblanceolate to oblong, and canescent (Jepson 1925; Reveal 1989; Hickman 1993). The predominantly sessile, single-flowered involucres are more or less openly distributed in small clusters (Munz and Keck 1959) at branchlet ends (Jepson 1925) and are urn-shaped, 1.5–2 mm long, grayish pubescent, bearing six bracts and three awns (Reveal 1989). In the SFVS, these involucral awns are straight rather than hooked, a trait that distinguishes *C. p.* var. *fernandina* from the more widely distributed *C. p.* var. *parryi* (Reveal 1989).

The sessile flowers are 2.5–3 mm long with a greenish-white tube and 6 white, sparsely hairy lobes, occurring in two series of 3 (Reveal 1989; Hickman 1993). Filaments and anthers of the nine stamens are white (Reveal 1989), whereas the pollen varies from white to pink. The pollen is heteromorphic (i.e., pollen wall sculpturing within a single pollen grain varies), a characteristic found in only eight taxa within the genus (Russell 2003). The significance of such sculpturing is unknown. The ovary is glabrous (Jepson 1925) and bears three styles with dry stigmas (Reveal 1989). Nectar is present around the base of the ovary and between the filaments. The flowers are protandrous (Taylor-Taft 2003) and are produced in late spring, April–June (Munz and Keck 1959). The fruit is a brown achene, 2.5–3 mm long with a 3-angled beak (Reveal 1989). Seeds of the genus *Chorizanthe* are reported to contain a straight embryo and abundant endosperm (Reveal 1989). Voucher SFVS specimens were deposited in the Fay A. MacFadden Herbarium (MACF) at California State University, Fullerton, California.

Study Sites

Investigations were first carried out in 2001 at the Ahmanson Ranch, the initial rediscovery site, located in the southeastern corner of Ventura County, California (Fig. 2). SFVS populations are found primarily on the slopes of Laskey Mesa and in isolated areas on the Mesa itself. Plants usually occur within open areas free of a significant number of competing species and are generally associated with San Andreas soils. These soils are composed of fine particles, soft sandstone, and loose sandy gravelly deposits (Glenn Lukos Associates Inc. 1999).

The specific study locations (GPS coordinates: 34°10.360′N, 118°40.839′W to 34°10.473′N, 118°40.277′W; Fig. 2) were selected because they contained abundant SFVS. Each site is characterized by having mostly barren soil, surrounded by coastal sage scrub communities, which are often substantially invaded by annual Mediterranean grasses and ruderals. Of the five sites chosen, four occur on southwest-facing slopes and the fifth occurs nearby on the mesa proper.

Subsequent investigations were completed in 2004 at the Newhall Ranch located in Los Angeles County, California (Fig. 3). The specific study locations (34°24.743′N, 118°37.786′W to 34°25.975′N, 118°35.044′W; Fig. 3) were selected

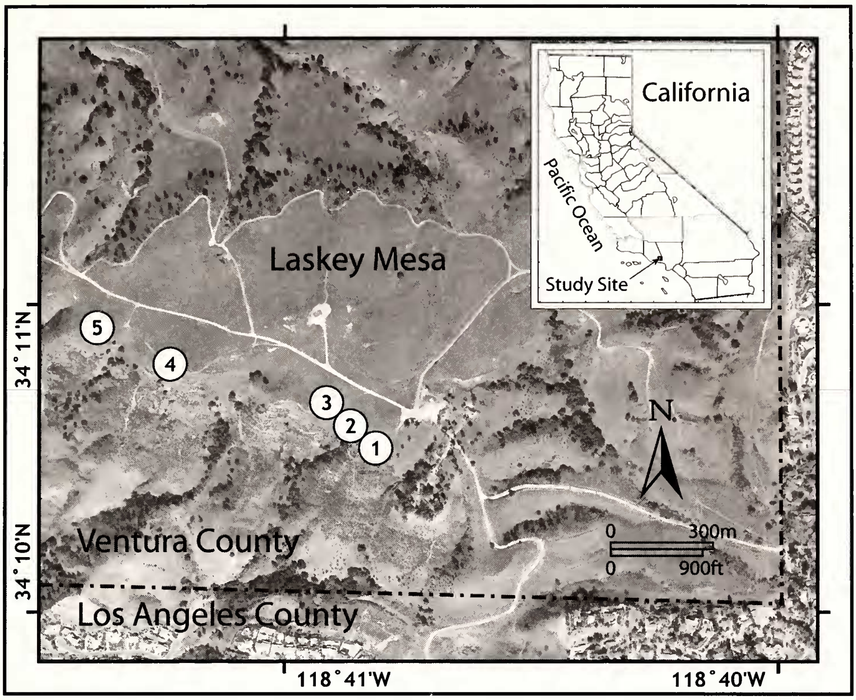

FIG. 2. Approximate locations of study sites on Laskey Mesa, Ahmanson Ranch. Aerial map for this figure provided by Terraserver/Globexplorer, (copyright 2005; used with permission).

because they had sufficient numbers of SFVS for observational requirements. Again, each site is characterized by supporting sparsely vegetated areas containing some bare ground and light litter, surrounded by coastal sage scrub communities, again with a substantial non-native annual grass component. Of the areas chosen for study, site 1 at the Grapevine Mesa is located on a west facing slope, site 2 at Airport Mesa is on a southwest facing slope, and site 3 at the Magic Mountain area is on a southeastern facing slope (Fig. 3).

Dawn-to-Dusk Observations

Ahmanson Ranch. Limited pollinator availability has proven to be a problem in some arid zone rare plants. To determine if pollinators are limiting reproductive success in the SFVS, we examined pollinator behavior, diversity, and the relative importance of each of the major pollinator groups by employing a series of dawn-to-dusk surveys that were conducted during the early (from 20 April through 22 April 2001), mid- (4 May through 6 May 2001) and late (18 May through 20 May 2001) bloom of the SFVS at three separate study sites (1, 2, and 4; Fig. 2) on the slopes of Laskey Mesa, Ahmanson Ranch. A total of 126 hr of dawn to dusk observations were completed during three observation periods (42 hr each during the early, mid and late seasons).

For the purposes of this study, early bloom is defined as the time when approximately 25% of the SFVS plants were in flower, mid-bloom as the time when at least 50% of the SFVS plants were in flower, and late bloom as the time when approximately 75% of the SFVS plants had completed flowering. Dawn-to-dusk means that the possible pollinators visiting SFVS plants were observed during at least 10 min out of each hour beginning on the hour after sun up and continuing throughout the day until 50 min after the hour before sun down. Each survey involved three consecutive days of observation.

At each of the three study sites, three subpopulations (e.g., 1A, 1B, and 1C) were selected on the basis of the ease with which one person could observe a sizeable number of plants simultaneously. One observer was assigned to each of the three separate study sites at the Ahmanson Ranch and, later, to the three Newhall Ranch study locations as well. That person observed and recorded the visitors to the SFVS plants in the initial subpopulation (e.g., 1A) during the first 10 min of each hour. That same observer then had 10 min to move to the second subpopulation (1B) where visitors were observed and recorded from 20 min after the hour until half past the hour. Finally, that same observer then rotated to the third subpopulation (1C) and repeated the process from 40 min after the hour until 50 min after the hour.

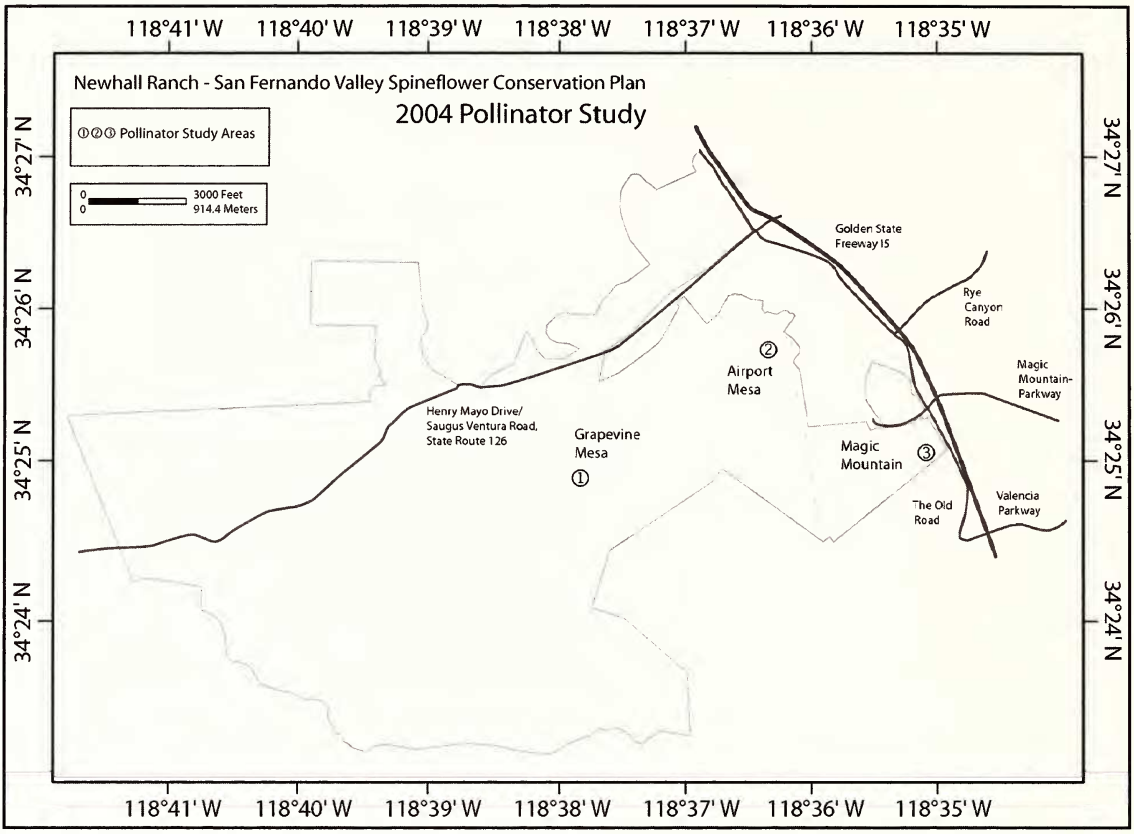

FIG. 3. Specific locations of sites investigated on the Newhall Ranch in Los Angeles County. Names for the Study Sites are: 1—Grapevine Mesa Site, 2—Airport Mesa South Site, and 3—Magic Mountain Site.

For the purposes of this study, a "visitor" was defined as any organism that actually landed on and came into contact with the anther(s) and/or the stigma(s) of the flower. "Visits" were defined as the number of times that a particular visitor landed on a SFVS flower and probed that flower for nectar and/or pollen. Data were subsequently analyzed in terms of number of visits and visitors. Diurnal temperatures were measured with a digital, indoor/outdoor thermometer (Digital Thermo-Clock, available from Oregon Instruments, P.O. Box 1190, Cannon Beach, OR 97110).

Newhall Ranch. Subsequently, similar dawn-to-dusk surveys were completed twice during the blooming period (from 23 April through 25 April 2004 and 7 May through 9 May 2004) of the SFVS at three separate study sites at the Newhall Ranch. These latter observations were conducted only during the mid- and late-bloom periods of the SFVS because 2004 was a very dry year (only about 19.1 cm of rainfall versus 54.6 cm in 2001), whereas the 95 yr average for this area is 47.3 cm) and many fewer plants were available for study and because those that were available flowered earlier and for a shorter period of time than had the plants at the Ahmanson Ranch in 2001. Based on the results of SFVS investigations at the Ahmanson Ranch, dawn-to-dusk observations were conducted at the Newhall Ranch between the hours of 9:00 a.m. and 7:00 p.m. (Jones et al. 2002). A total of 90 hr of dawn to dusk observations were completed during three observation periods (30 hr each during the early, mid and late seasons). All other details related to how the surveys were conducted were identical to those at the Ahmanson Ranch.

Pollinator Collection and Identification

Ahmanson Ranch. Representative samples of visitors were collected on 20–22 April and 4–6 and 18–20 May between 10:00 and 17:00. Sampling was primarily conducted at a different location (Site 5; see Fig. 2) than those used for the dawn-to-dusk observations in order to eliminate the possibility of decreasing pollinator visitations through collection. Organisms seen visiting three or more flowers were captured in an insect net or by using a blowing aspirator and placed in killing jars charged with ethyl acetate. Each individual was then placed in a vial with 70% ethyl alcohol.

Newhall Ranch. To determine if there was a positive association between the invertebrate community in the vicinity of the SFVS and actual visitors to the SFVS, thus indicating the extent to which the SFVS was being visited by the potential vectors available in the specific area where the plants were located, we set up a time based sampling method to capture these potential pollinators. Individual insects that were on or in the area of the SFVS were collected using aspirators and nets. Samples were collected for a total of 30 person minutes at each site and each captured individual was placed into a glassine envelope. Collections were primarily conducted at a location (subpopulation) near, but not within, the dawn-to-dusk study subpopulations at each of the three sites. Again, this was done in order to eliminate the possibility of decreasing pollinator visitations as a result of collection. One sample was collected on April 23rd, three on May 7th, and three on May 8th, 2004. For analysis, these were pooled for a single site for a single day. For each insect collected, we noted whether it was found on or near the SFVS.

We also employed pitfall traps to sample ground dwelling arthropods. Each trap consisted of a single 16 oz plastic cup filled with approximately 4 oz of propylene glycol to act as a preservative. Three traps were placed at each site, each covered with hardware mesh to prevent the capture of vertebrates. A single pitfall sample consisted of approximately 48 h of continuous trapping (from Friday afternoon until Sunday afternoon). Pitfall traps were open from the 23rd until the 25th of April and from the 7th until the 9th of May 2004.

All captured arthropods were identified to order, morphospecies, (this being essentially a recognizable taxonomic unit, see Oliver and Beattie 1993, 1996), or to species, if possible.

Pollen Analysis

Ahmanson Ranch. Visitors collected for identification were returned to the laboratory and the vials shaken to remove pollen from the body surface. The cap of each vial was removed and the ethyl alcohol was allowed to evaporate down to about a single drop. That drop was then placed on a slide and, following evaporation, cotton blue (1% aniline blue in lactophenol) was added to stain the pollen grains. Slides were viewed under a Leitz compound microscope where an a priori set minimum of 200 pollen grains were identified using reference slides. The number of plant species and pollen grains found on each individual visitor was used to determine which pollinators carried the pollen of SFVS and how constant they were to the SFVS. Pollinator constancy was defined on a percentage basis. The higher the percentage of one pollen species in a sample, the more specific that pollinator was to that particular plant species. For the purpose of this study, a pollinator was considered to be "constant" when that pollinator visited a given species at least 95% of the time during a single foraging flight. All captured visitors were examined and a determination was made of the pollen they were carrying.

Newhall Ranch. Each visitor captured while visiting at least three flowers was examined under a Bausch and Lomb dissecting microscope to see if pollen was present on the visitor and, if so, where it was located. A 3 cm piece of double sided Scotch tape with one end cut to a point. The pointed end was used to pick up any available pollen from the visitors under the dissecting scope. Once the pollen had been transferred from the visitor to the double-sided tape, the tape was placed on a 7.62 cm × 2.54 cm × 1 mm glass microscope slide. One or two drops of cotton blue were then added to stain the pollen grains and the slide allowed to sit for at least 24 hrs before examination. Slides were viewed under a Leitz compound microscope and were identified using reference slides (prepared with known SFVS pollen using the identical staining technique). Types and numbers of pollen grains recovered from each individual were used to determine which pollinators carry the pollen of SFVS and how constant they were to the SFVS.

Exclusion Experiments

Exclusion or bagging experiments were at conducted at Ahmanson Ranch at Site 3 (on the Mesa) to determine whether the SFVS requires a vector to facilitate the pollination process and to determine the relative importance of ants and other crawling insects as pollinators. The bagging experiments were set up on 7 April 2001 along an old dirt road selected to minimize possible destruction of SFVS plants since the experimental design required the use of well-separated plants. Prior to blooming, 30 plants were selected haphazardly to serve as controls (Control 1). Another 30 plants were selected and surrounded by Tangle-Trap® (Insect Trap Coating Brand, the Tanglefoot Company, Grand Rapids, Michigan 49504) to prevent any terrestrial pollinators from reaching the flowers. This series, termed "Experimental" (ant free), served to determine the role of flying versus crawling insects (primarily ants) as pollinators. A third set of 30 plants was covered with a wire cage screened with nylon and secured to the substrate with u-shaped sections of wire. The base of these cages was also surrounded with Tangle-Trap®. This latter series, which excluded both crawling and flying insects, was used to determine if the SFVS is self-pollinated and was termed "Self".

These last two sets of 30 plants (Experimental and Self) were initially also surrounded by concentric rings of cinnamon (suggested as an environmentally friendly barrier) as well as Tangle-Trap®, with cinnamon on the inner ring. This practice was abandoned approximately half way through the experiments since the cinnamon appeared to be toxic to plant leaves coming into contact with it.

A final group (fourth set) of 30 representative plants was selected haphazardly to serve as an additional (second) set of controls (Control 2). This set became necessary when it was noted that the originally selected control plants were somewhat smaller than the two series of experimental plants. All plants chosen were evenly distributed along a plot approximately 115 m long by 3 m wide. Individual plants located more than 8 cm from the closest SFVS neighbor were chosen for the self-pollination treatment and the experimental treatment to allow room for the Tangle-Trap® layer without having to sacrifice surrounding plants. Tangle-Trap® was renewed weekly.

After the plants set fruit, they were harvested, placed in paper bags, and returned to the laboratory. Fruits were then removed from their involucres and a minimum of 200 involucres was sampled from each plant to determine fruit set for each treatment and the controls. Data were analyzed using ANOVA (Tukey's multiple comparison procedure) in Minitab version 13.31 (Minitab, Inc., State College, PA 16801-3008). To test if the exposure to cinnamon affected fruit set, each of the plants exposed to cinnamon was divided into two portions. Fruit set on the inner half (older portions of the plant, exposed to cinnamon) was compared to fruit set on the outer half (younger part of the plant, not exposed to cinnamon) using a paired t-test.

Nectar Availability

In order to provide information on the nectar rewards being presented to visitors at Ahmanson Ranch, one µl microcapillary tubes were carefully inserted into 20 flowers on each of 23 separate plants at Site 3 on 14 May 2001. The flowers to be sampled on each of the selected plants were carefully enclosed within nylon bags the previous day to ensure that no nectar was removed by visitors prior to the sampling procedure. Only newly opened flowers were sampled. Microcapillary tubes were placed in 4 dram glass screw-cap vials and transported to the laboratory for measurement. The amount of nectar in each microcapillary tube was measured under a Bausch and Lomb dissecting microscope and the amount of nectar produced per flower was calculated.

To determine any possible diurnal pattern of SFVS nectar production, mature plants grown in 1 gallon pots at the California State University, Fullerton, greenhouse complex were sampled. These plants were in the later phase of flowering and open flowers had been exposed to pollen vectors prior to this study. Sixty hours before observation, several branch portions on each plant were enclosed in nylon bags to exclude pollinators. On 1 July 2001, six plants were moved into the greenhouse, placed in an exclusion room, and the bags partially removed to allow access to the newly opened flowers. Nectar sampling was conducted at 9:00, 13:00, and 17:00. At the initial sampling time, nectar was collected from 20 flowers, 10 each on two separate plants. At 13:00, flowers on these two plants were resampled and 20 flowers on two new plants were also sampled. Finally, at 17:00, all flowers were re-sampled and 20 more flowers on two additional plants were sampled. Nectar was sampled with one µl microcapillary tubes from open flowers only.

Seed Germination

Representative SFVS seeds were collected on 10 July 2001 from plants at Ahmanson Ranch Study Site 5. Fruits were sampled from the distal portions of flowering branches. All seeds were cleaned and removed from the surrounding floral remains to ensure that only whole seeds were being tested. Except where noted, all seed treatments were placed in an unheated greenhouse under ambient light in Petri dishes with one sheet of Whatman No. 1 filter paper. Dishes were watered with reverse osmosis (RO) water as needed. Germination was defined as the emergence of the embryonic root or radicle. Samples of 50 seeds each (except for Treatment 2 where 51 seeds were used) were tested in the following ways:

1) Control.
2) Leach 24 hr: seeds leached 24 hr under running tap water, then placed in a Petri dish.
3) Leach and Stratify: seeds leached 24 hr, placed in a Petri dish, then stratified for 2 wk in a refrigerator at 3–4°C.
4) Stratify Only: seeds sown directly in a Petri dish, then stratified for 2 wk in a refrigerator at 3–4°C.
5) Direct Planting: seeds sown in a layer of sand on top of greenhouse soil mix in plastic flower pots, watered until soaked, then placed on outside benches. Pots were watered as necessary to keep the sand from drying out. This treatment served as a supplementary control and was used to determine the basic non-treatment viability of the seeds.

The time interval for these germination tests was approximately six weeks for seeds that were

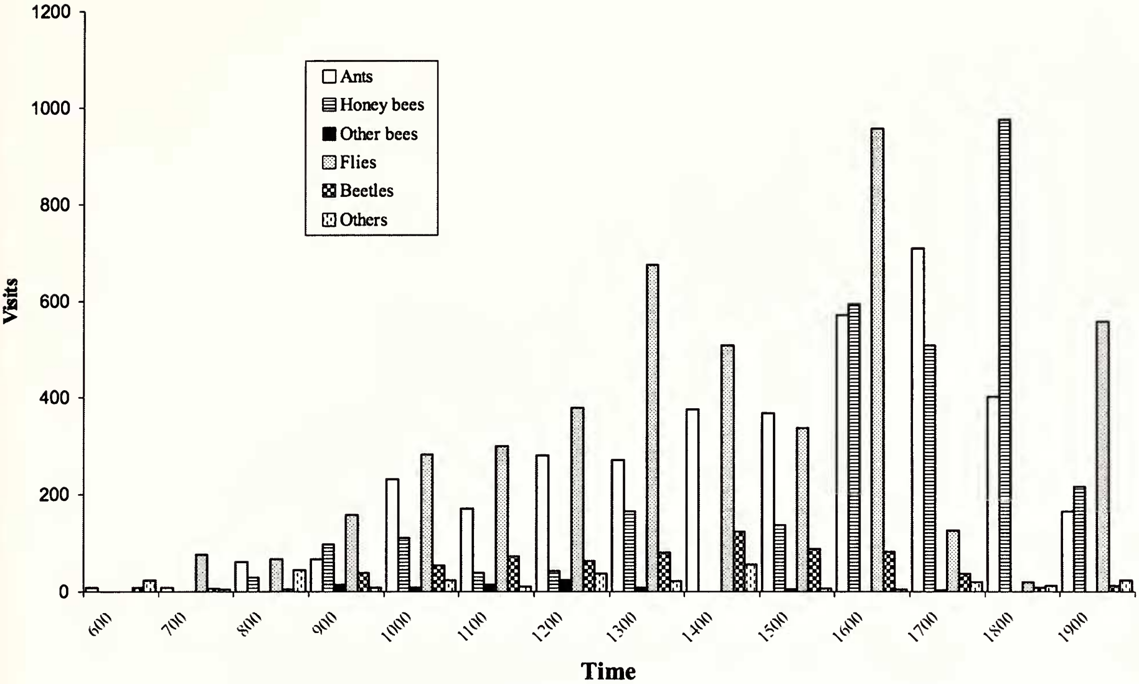

FIG. 4. Total dawn-to-dusk visits observed, by hour, during all observation periods for the major visitor groups at all study sites at the Ahmanson Ranch during the 2001 SFVS flowering season.

subjected to the stratification treatments and three weeks for all other treatments.

RESULTS

Dawn-to-Dusk Observations

Ahmanson Ranch. The results of these dawn-to-dusk observations are summarized in Fig. 4. It is apparent that this herbaceous plant received numerous visits (total of 9816) from a wide range of invertebrate organisms; however, among the invertebrate groups, five species accounted for nearly 75% of all visits made to the SFVS. These included: two species of ants, *Dorymyrmex insanus* Roger (37.8%) and *Solenopsis xylonii* McCook (2.6%) (Hymenoptera: Formicidae); two species of beetles, *Zabrotes* sp. (1.9%) (Coleoptera: Bruchidae: Amblycerinae), and *Emmenotarsis quadricollis* LeConte (2.4%) (Coleoptera: Melyridae: Dasytinae [identification tentative]); and the European honey bee, *Apis mellifera* (30.3%) (Hymenoptera: Apidae). Other taxa captured on the flowers of the SFVS at the Ahmanson Ranch included Diptera in the families Bombylidae, Syrphidae, Calliphoridae, Sarcophagidae, and Tachinidae, Hymenoptera in the families Ichneumonidae, Chrysididae, Sphecidae, Halictidae, Andrenidae, Megachilidae, Pompilidae, Vespidae, and Formicidae, and Lepidoptera in the families Riodinidae and Hesperiidae.

Early season.—We performed detailed analyses on each of the early, mid- and late seasons and for all three seasons combined. The total number of individual visitors (hereafter referred to as visitors) and the total number of flower visits (hereafter referred to as visits) by each were analyzed separately (Figs. 5 and 6).

In terms of visits, an analysis of the early (20–22 April 2001) series of observations (Fig. 5) showed that of the 1662 visits were made by

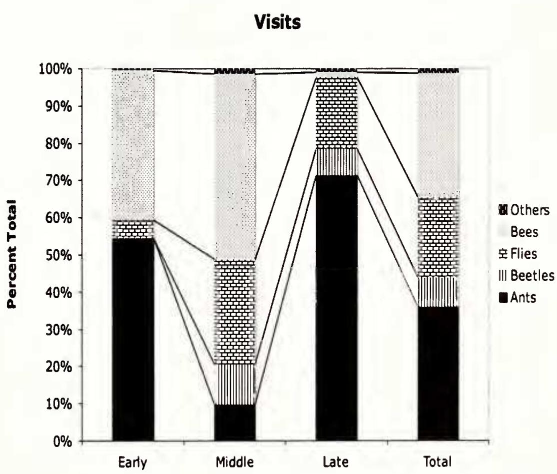

FIG. 5. Summary of the early (n = 1662), middle (n = 5184), late (n = 2984), and total season (n = 9830) SFVS visits recorded during dawn-to-dusk observations at the Ahmanson Ranch in 2001.

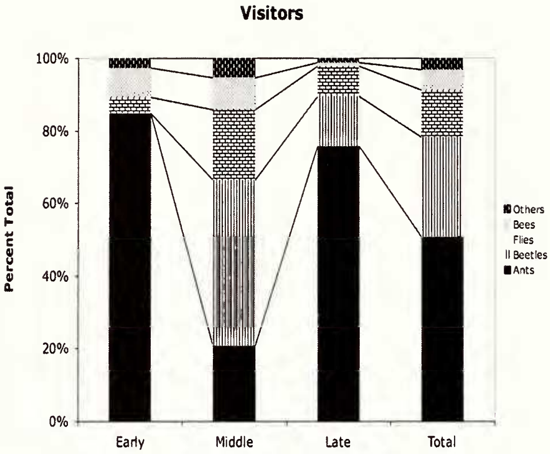

FIG. 6. Summary of the early (n = 179), middle (n = 804), late (n = 710), and total season (n = 1693) SFVS visitors recorded during dawn-to-dusk observations at the Ahmanson Ranch in 2001.

various invertebrates of which >54% were made by ants and 40% were by bees nearly all of which were made by *Apis mellifera*.

Further, of the 179 individual visitors observed during the early bloom (see Fig. 6), ants were dominant (84%). Among the ants, the dominant species was *Dorymyrmex insanus*, which accounted for 74% of the visitors. *Apis mellifera* accounted for 7% of the total visitors during this early portion of the blooming season.

Mid-season.—Regarding visits, an analysis of the middle (4–6 May 2001) series of observations (Fig. 5) showed that of the 5184 visits by various invertebrates, of which 49% were by bees, the vast majority of those were made by *Apis mellifera*.

Additionally, of the 804 individual visitors observed during the mid-blooming period (Fig. 6), 21% were ants, 46% were beetles, 19% were flies, and 9% were bees, of which 6% were *Apis mellifera*. Among the ants, significant visitors were *Dorymyrmex insanus* (9.3%) and *Solenopsis xylonii* (8.1%).

Late season.—Again, in terms of visits, an analysis of the late series of observations (Fig. 5) revealed that of the 2984 visits by various invertebrates, dominated by ants (71%).

Of the 710 individual invertebrate visitors (Fig. 6), 77% were made by ants. Among the ants, the dominant species was *Dorymyrmex insanus*, which accounted for 71% of all visitors during the late SFVS blooming season.

Entire flowering season.—If all visit data from early, mid-, and late season sampling periods are combined for the three study sites (Fig. 5), the total number recorded is 9830. Visits by ants accounted for 37% of this total, while 8% were made by beetles, and 55% were made by all other invertebrates. Within this latter group (55%), more than 38% were made by flies and more than 59% were made by bees. Of the bee visits, 90% were made by *Apis mellifera*.

Of the 1693 visitors noted throughout the season (Fig. 6), 51% were ants, 27% were beetles, 13% were flies, and 6% were bees.

It is interesting to note that the greatest number of visits (5184) and visitors (804) was recorded during the mid-blooming period (4–6 May 2001) when the vast majority of the SFVS plants were in full bloom. This compares to 1662 visits and 179 visitors during the early bloom (20–22 April 2001) and 2984 visits and 710 visitors during the late bloom (18–20 May 2001).

Newhall Ranch. Visitors to the flowers of the SFVS at the Newhall Ranch were dominated by one species of ant, *Forelius mccooki*, and flower beetles in the family Melyridae (unknown Dasytinae). Together these taxa made up nearly 50% of all floral visitors to the SFVS at the Newhall Ranch. Besides these dominant taxa, other species captured on the flowers of the SFVS at the Newhall Ranch included representatives from the Coleoptera in the family Bruchidae, Diptera in the families Bombylidae, Syrphidae, Calliphoridae, Sarcophagidae, and Tachinidae, Hymenoptera in the families Chrysididae, Sphecidae, Halictidae, Megachilidae, Pompilidae, Vespidae, and Formicidae, and Lepidoptera in the family Riodinidae.

Mid-season.—An examination of the visits made by each of the visitor groups observed during the mid-season period (23–25 April 2004) shows that flies (79%) greatly outnumbered beetles (16%) in terms of the number of flowers actually visited by individual visitors at Site 1. Flies (67%) also dominated the visits at Site 2, followed by beetles (11.5%) and ants (11%). Ants (61%) made the most numerous visits at Site 3 followed by beetles (32%). Total visits varied among the three sites from 2021 at Site 1, 633 at Site 2, and 2488 at Site 3. Overall, 5142 visits were made to SFVS flowers during the mid-season flowering period. During that time, flies (40%) dominated the floral visits, followed by ants (33%) and beetles (23%; Fig. 7).

Visitors to the flowers of the SFVS varied substantially among the three study sites during the mid-season. Flies (67%) and beetles (27%) dominated the visitors at Site 1 and at Site 2 (58.5% for flies and 21.5% for beetles), whereas flies were replaced by ants (43%) as dominant visitors along with beetles (42%) at Site 3. Total visitors also varied considerably among the sites, with 722 visitors at Site 1, 130 at Site 2, and 483 at Site 3. Overall, 1335 visitors were observed on the flowers of the SFVS during the mid-season flowering period. During this period, flies (42.5%) beetles (32%), and ants (20%) were the dominant SFVS floral visitors (Fig. 8). Observa-

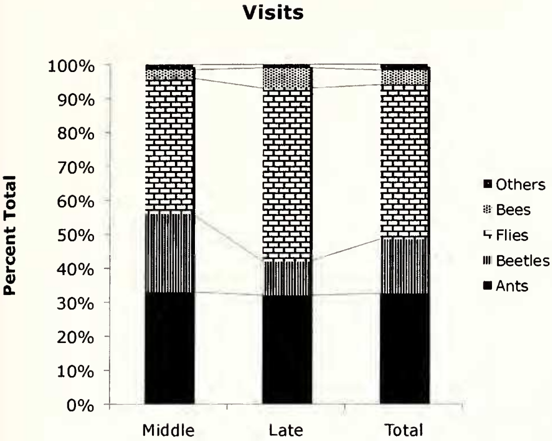

FIG. 7. Summary of mid-season (n = 5142), late season (n = 2864), and total (n = 8006) visits recorded during dawn-to-dusk observations at the Newhall Ranch in 2004.

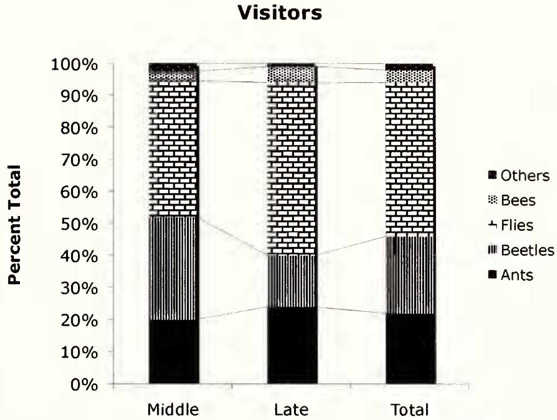

FIG. 8. Summary of mid-season (n = 1335), late season (n = 733), and total (n = 2068) SFVS visitors recorded during dawn-to-dusk observations at the Newhall Ranch in 2004.

tions of interest include the total lack of honey bee visitors and the variation in ant species present at each location.

Late season.—An examination of the number of flowers visited during the late season observations (7–9 May 2004) by each of the visitor groups shows that flies (90%) greatly outnumbered beetles (6.5%) at Site 1. Flies (31%), beetles (28%), ants (25%), and bees (15%) almost equally dominated the visits at Site 2 (Fig. 7). Ants (78%) made the most numerous visits at Site 3, followed by bees (11%) and beetles (9%). Total visits varied among the three sites with 1483 at Site 1, 372 at Site 2, and 1009 at Site 3. Overall 2864 visits, or about half the number of visits seen during the mid-season, were made by the visitors to the flowers of the SFVS during the late season flowering period. During this late season, flies (51%) dominated the floral visits, followed by ants (32%) and beetles (10%; Fig. 7).

Visitors to the flowers of the SFVS also varied substantially from site to site during our late-season observations. Flies (83%) dominated the visitors at Site 1, followed by beetles (12%). At Site 2 there was a more equal distribution of visitors with beetles (31%), ants (28%), flies (25.5%) being the dominant visitors, whereas ants (70%) were by far the dominant visitors at Site 3. Total visitors also varied considerably among the sites, with 429 visitors at Site 1, 133 at Site 2, and 171 at Site 3. Overall, 733 visitors, or about half the number of visitors seen during the mid-season, were observed on SFVS flowers. During this late season, flies (54%) dominated the floral visitors, followed by ants (24%) and beetles (16%; Fig. 8).

Entire flowering season.—If all the data from the mid- and late season sampling periods are combined for the three study sites (Fig. 7), the total number of recorded visits is 8006, which is reasonably close to the total number of visits (8168) recorded during the mid- and late flowering periods of study at the Ahmanson site, even though the 2004 season was a much drier year that produced many fewer individual plants. Flies dominated the floral visits (45.5%), followed by ants (32.5%) and beetles (16%). Bees, especially honey bees, were not well represented among the visitors to the flowers of the SFVS during the entire blooming period.

Total visitors also varied considerably among the sites. Overall, 2068 visitors were observed on the flowers of the SFVS during the mid-season flowering period (Fig. 8). During this period, flies (42.5%) dominated the floral visitors, followed by beetles (32%) and ants (20%).

Pollinator Collection and Identification

Ahmanson Ranch. Identified visitors to the SFVS, collected primarily at Study Site 5, included 5 species of beetles, 20 species of flies, 3 species of butterflies, and 27 species of bees, ants, wasps, and their relatives. For a complete list of visitors, contact CEJ via email. These were all captured on the flowers of the SFVS.

Newhall Ranch. In total, we captured 4223 individuals on the SFVS flowers and the adjacent coastal sage scrub community. This sample consisted of 12 different insect orders, two arachnid orders (Acarina and Araneae), one myriapod (Chilopoda), one crustacean (Isopoda), and a large number of Collembola (Fig. 9). Non-insect taxa made up a large portion of the sample (2267 individuals). In particular, 45% of the sample was made up of Collembola.

Taxa representing 7 different insect orders were captured on or in close proximity to the SFVS

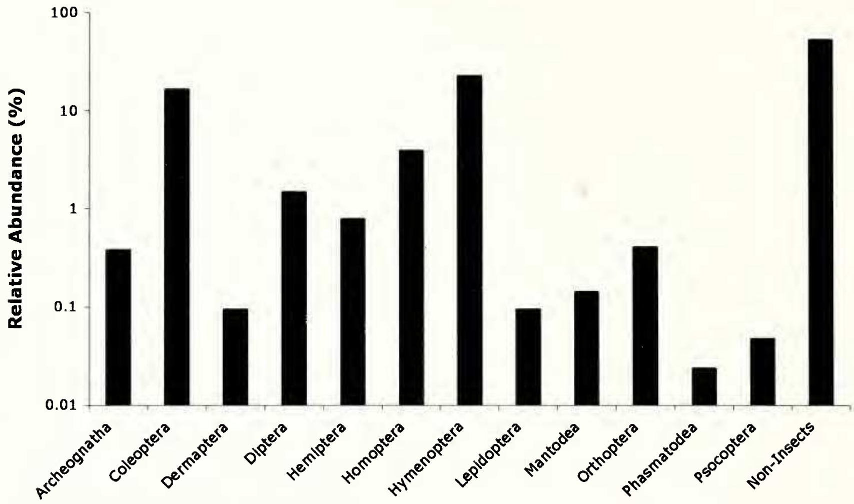

FIG. 9. Relative abundance of different invertebrate taxa captured at Newhall Ranch. These taxa were collected on the flowers and, also in the surrounding coastal sage scrub community.

flowers (Fig. 10). These same 7 orders were also found in the surrounding coastal sage scrub community (a total of 1912 individuals, Fig. 10). The relative abundance of the insects captured on the flowers (44 individuals) is largely reflective of their relative abundance in the surrounding coastal sage scrub community (R^2 = 0.9337; Fig. 11).

In terms of the insect species diversity observed at the Newhall Ranch, we identified 101 different morphospecies. Hymenopterans (bees and ants) were the most diverse order of insects, followed by Dipterans (flies), Coleopterans (beetles), and Hemipterans (true bugs) (Table 1). The most abundant orders were generally the most diverse.

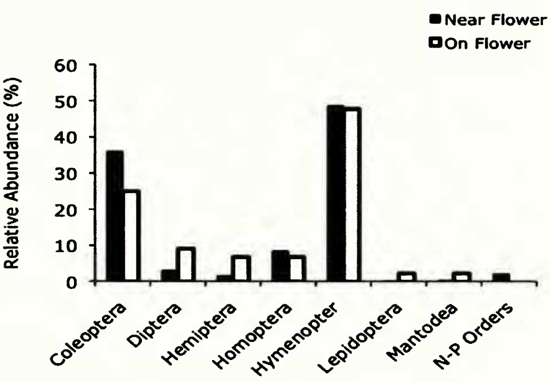

FIG. 10. Insect community composition (relative abundance) of different insect orders captured on flowers and near flowers. The near flowers sample includes data from pitfall traps and hand collected individuals. Non-Pollinator (NP) orders includes groups that were never observed on SFVS (Archeognatha, Dermaptera, Phasmatodea, Orthoptera, and Psocoptera). This group makes up only 3% of the entire sample.

Of the 101 different morphospecies, 49% are represented by a single specimen and 16% by two specimens. Only in 7 morphospecies did we collect 50 or more individuals (Fig. 12). These data indicate that there are a number of infrequent species present and very few abundant species. These data were only recorded at Newhall Ranch and were not taken at Ahmanson Ranch.

The taxa of fauna collected varied with the sampling method. Pitfall traps primarily capture active ground-dwelling arthropods and tend to underestimate the abundance of inactive or non-ground dwelling species (e.g., Adis 1979; Spence and Niemelä 1994; Work et al. 2002). Using pitfall traps, we captured 1665 individuals from 69 different morphospecies and from hand-collecting we captured 291 individuals from 51

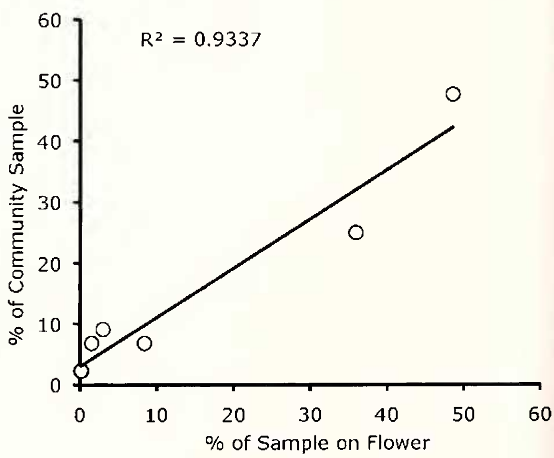

FIG. 11. Relationship between the relative abundance of taxa captured on the spine flower and their relative abundance in the community (R^2 = 0.9663, $P < 0.05$).

TABLE 1. DISTRIBUTION OF MORPHOSPECIES COLLECTED ACROSS INSECT ORDERS.

Order	Number of morphospecies
Hymenoptera	31
Diptera	18
Coleoptera	15
Hemiptera	14
Homoptera	7
Orthoptera	6
Lepidoptera	3
Archeognatha	2
Psocoptera	1
Phasmatodea	1
Dermaptera	1

different morphospecies. Results of the two sampling methods share only 21 species in common (Jaccard Coefficient = 0.21). In addition, based on species accumulation curves (Colwell and Coddington 1994), we have sampled the species captured with pitfall traps much more thoroughly than the species we collected by hand (Fig. 13). This is evident since the species accumulation curve for the hand collection is essentially linear whereas the pitfall species accumulation curve is hyperbolic and the rate of species accumulation has decreased. Since pollinator diversity was estimated using only hand-collected individuals, it is possible that we have underestimated the number of pollinator species.

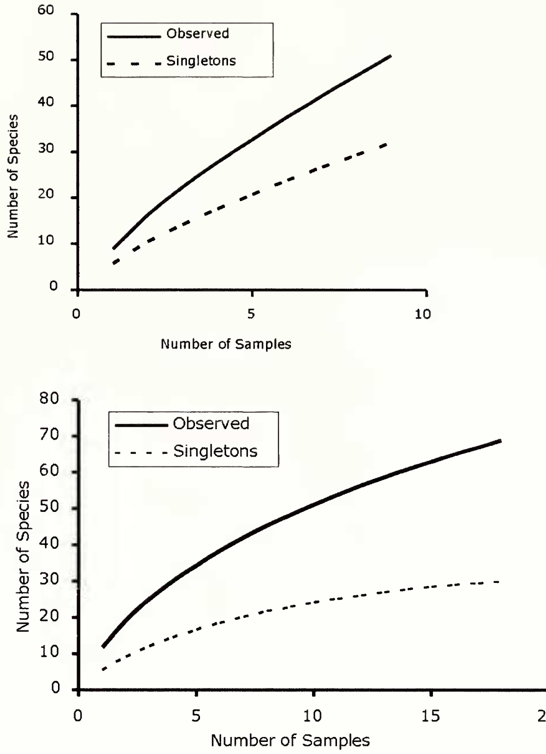

FIG. 13. Species accumulation curves for pitfall trapped (upper) and hand collected (lower) samples. Singletons are species represented by a single specimen.

Pollen Analysis and Constancy

Ahmanson Ranch. Of all insect floral visitor specimens captured, only those of *Apis mellifera* were captured in sufficient numbers and had enough pollen lodged on their bodies (an a priori set number of 200 pollen grains was established as an adequate subsample to examine from each specimen) to carry out a complete analysis of the degree of their constancy to the SFVS. Data on the purity of pollen loads was collected from 10 different individuals of *Apis mellifera*. In all but one case, these honeybees were very constant to the SFVS with constancy levels ranging between 96–99%. The one exception carried only 59% SFVS pollen. Overall, the pollen loads on *Apis mellifera* averaged 94% (SD = 12.4) SFVS pollen and an average of 4.5% (SD = 2.1) other pollen species per sample.

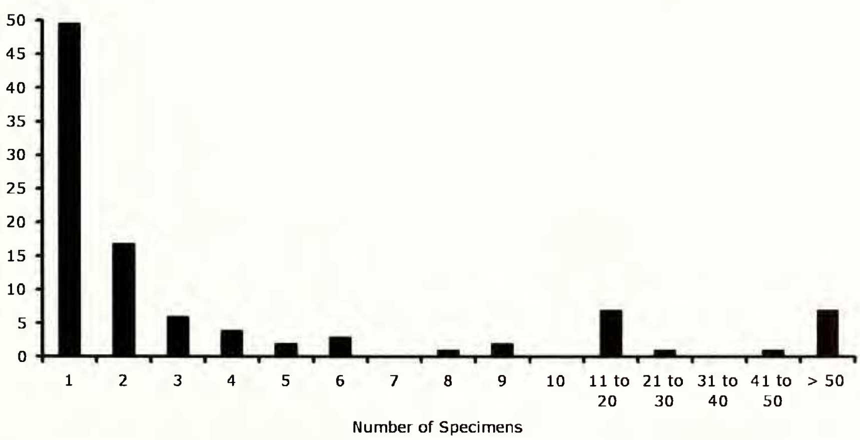

FIG. 12. Number of individuals collected of each species.

The remaining taxa visiting the flowers of the SFVS either did not carry at least 200 pollen grains or their sample size was less than three, an examination of the pollen loads of these visitors was completed to determine their specificity to the SFVS flowers. Of the non-honeybee visitors captured while visiting the SFVS flowers, 56 carried one or more pollen grains in general (see Jones et al. 2004). Of those 56, 48 (86%) carried one or more pollen grains of the SFVS. Of the 48 that carried pollen of the SFVS, 28 (58%) carried only SFVS pollen. The average constancy for all 48 specimens that carried at least one pollen grain of the SFVS was 87%, with the range varying from 1.6 to 100%.

The constancy for the most abundant visitor recorded on the SFVS flowers at the Ahmanson Ranch, *Dorymyrmex insanus*, was 100%; however, we had only a sample of two individuals. These two carried 10 and 9 pollen grains of the SFVS respectively. Five individuals of *Solenopsis xylonii*, another prominent ant visitor to the flowers of the SFVS, also proved to be carrying SFVS pollen (between 8 and 37 pollen grains) and exhibited an average constancy of 98%. The average constancy exhibited by all ants was 98% and ranged from 89 to 100%.

Newhall Ranch. The 43 insect floral visitors caught while visiting the SFVS represented at least 14 different species of potential pollinators. Of those 43, 58% carried pollen loads of one or more pollen grains. The 25 floral visitors that carried pollen loads represented at least 10 different taxa of potential pollinators. Of these, 72% carried only SFVS pollen, whereas the remainder carried mixed pollen loads, but all included some pollen from the SFVS (for a complete list of the individual species, contact CEJ via email).

Of the 17 individuals of the small red ant species *Forelius mccooki*, caught on the SFVS flowers and sampled for pollen, 76.5% carried one or more SFVS pollen grains. Of the 13 that carried pollen, 69% carried only SFVS pollen. The remainder carried mixed loads, but all included some pollen of the SFVS.

Exclusion Experiments

Regarding the two sets of plants exposed to cinnamon, no significant difference was found between the number of fruits produced on the inner half of the plants and the outer portion (t-test Control I, t = 0.2554, P > 0.8; Control II, t = 0.2713, P > 0.8; Experimental (without ants), t = 0.307, P = >0.8; and Self, t = 0.2413, P > 0.8; in all cases n = 5, df = 4), thus indicating that the cinnamon layer did not affect fruit set and, therefore, that there was no difference in efficiency of pollination of the plants throughout the duration of the experiment.

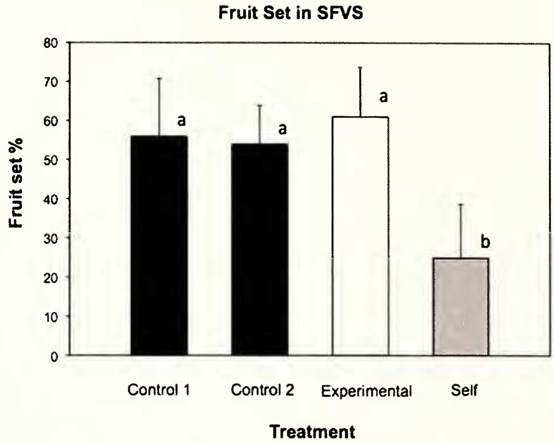

FIG. 14. Comparison of SFVS fruit set between the two sets of controls (Control 1, plants selected prior to the beginning of plant bloom, and Control 2, plants selected at the end of the experimental period. Treatment 'Experimental' excludes crawling insects, especially ants, and treatment 'Self' excludes all visitors. Percent fruit set is determined by dividing the total number of fruits set by the total number of flowers examined. Error bars indicate one standard deviation. Those marked "a" are not significantly different from one another but are significantly different from the Self, which is marked "b". ANOVA (f = 48.02, n = 119, P < 0.0001) followed by a Tukey's Test (q = 3.69, n = 119, df = 118, P < 0.01).

An analysis (ANOVA) of the fruit set in the two sets of controls and the two exclusion treatments (Fig. 14) showed a significant difference in fruit set among the two sets of Controls, the Experimental, in which crawling insects (such as ants) were prohibited from visiting the SFVS flowers, and the Self plants (f = 48.02, n = 119, P < 0.0001). Specifically, there was no significant difference between the two sets of Controls or between the Controls and the Experimental plants, but there was a significantly lower number of fruits produced by the selfing treatment (Tukey's multiple comparison, q = 3.69, n = 119, df = 118, P < 0.01).

Nectar Analysis

In the sampling of 460 bagged SFVS flowers (20 each on 23 separate plants), the average nectar production per flower was 0.0034 μl with a range from 0.0 to 0.014 μl per flower. Bee flowers normally have an average of 2.5 ± 1.1 μl per flower (Cruden et al. 1983). Insufficient nectar was produced for refractometer determinations of sugar content.

Nectar sampling to determine any possible diurnal pattern of nectar production is presented in Table 2. No measurable nectar was detected at the 9:00 sampling period. However, measurable nectar was collected in all afternoon samples.

TABLE 2. DIURNAL NECTAR PRODUCTION IN THE SFVS, AS MEASURED IN THE CSUF GREENHOUSE COMPLEX ON 1 JULY 2001. N = 20 flowers per plant sample.

	900 hrs—µl/fl	1300 hrs—µl/fl	1700 hrs—µl/fl
Plants 1 and 2	0.0000	0.00391	0.00344
Plants 3 and 4	—	0.00938	0.00234
Plants 5 and 6	—	—	0.00313
Average	0.0000	0.00664	0.00297

Calculated nectar values ranged from 0.00234 to 0.00938 µl per flower.

Seed Germination

The results of the seed germination tests are presented in Table 3. Germination in the Control seeds after 6 wk was 74% whereas germination in all other treatments was noticeably lower. In particular, stratification, either alone or in combination, decreased percent germination.

DISCUSSION

The reproductive biology of rare and endangered plants has been of great interest to biologists charged with developing successful management strategies for these species (Purdy et al. 1994; Schemske et al. 1994; Luijten et al. 1996; Bernardello et al. 1999; Kaye 1999; Timmerman-Erskine and Boyd 1999). This aspect of the conservation or reintroduction of rare species involves not only understanding the factors affecting seed production, but also factors affecting long-term successful propagation (Giblin and Hamilton 1999). In order for a population to remain stable, the plants must both flower and receive sufficient pollinators in order to produce viable seeds. Those seeds must then receive enough water and nutrients, avoid predation, and grow to mature flowering plants capable of producing the next generation. Interference with any of these steps will inhibit reproduction and, if consistent over time, may result in reduced populations (Kaye 1999). Results from this investigation establish an information base regarding the initial steps in the reproduction process of the SFVS that should prove useful to conservation biologists responsible for protecting this endangered taxon.

TABLE 3. SFVS SEED GERMINATION RESULTS AS OF 4 FEBRUARY 2002.

Treatment	Sample size (N)	Number germinated	% germination
Control	50	37	74
Leach 24 hr	51	22	44
Leach and stratify	50	9	18
Stratify only	50	5	10
Direct planting	50	25	50

Pollinator Diversity—Generalist Strategy

Data from the dawn-to-dusk visitor surveys at both the Ahmanson and Newhall Ranches are consistent with a generalist (both within and between years) rather than a specialist pollination vector strategy. We documented a wide variety of taxa, terrestrial as well as aerial (including a number of different species of ants, bees, beetles, and flies) that visit the SFVS flowers and would appear to be capable of effecting pollination with subsequent seed set. With the exception of one of the three species of ants that are frequent visitors to the flowers of the SFVS, we did not examine in any detail the efficiency of the various possible vectors at facilitating fruit set. Given that the ant visitors were among the most frequent to the flowers of the SFVS, we did examine the efficiency of the major ant visitor at Ahmanson Ranch (*Dorymyrmex insanus*) as a pollinator of the SFVS and this work is reported elsewhere (Jones et al. unpublished).

Both the Northern Hemisphere (annuals) and South American (mostly perennials) members of the genus *Chorizanthe* occupy xerophytic habitats in which rainfall is quite variable from year to year (Goodman 1934; Reveal and Hardham 1989). Such variation may favor the generalist pollination strategy that seems to be the rule for species in this genus. The generalist strategy has been found in all members of this genus that have received any attention regarding the pollinators that frequent their flowers (Reveal and Hardham 1989; Bauder 2000; U.S. Fish and Wildlife Service 2001; Murphy 2003).

Specialization of pollinators has been a key concept of plant-pollinator coevolutionary models (Thompson 1994). This assumption is based on the "most effective pollinator principle", which states that natural selection should proceed toward floral phenotypes that attract a limited spectrum of potential pollinators and result in an increase in the effectiveness of fruit set in the plant (Stebbins 1970). This process by which the flowers are molded by a small group of related and effective pollinators is referred to as "adaptive specialization" (Thompson 1994; Herrera 1996; Johnson and Steiner 2000).

Although this principle has often been used as the underlining support for the idea that evolution should proceed toward more specialized mutualistic associations between specific flowers and their pollinators, Stebbins (1970) emphases that this refers to the "predominate and most effective vector" and does not mean that the plant is "pollinated exclusively by this vector," and as such, supports the concept of pollinator syndromes. In other words, by this "principle", a plant species should have one or only a few related primary pollination vectors (e.g., two or more bee species with similar morphologies and behaviors would fall into the bee pollination syndrome—melittophily of Faegri and van der Pijl 1971), but certainly can have a few to several other pollinators as well. In fact, as pointed out by Futuyma (2001), there is a continuum between species that are exclusive specialists pollinated by only a single vector species to species that are pollinated by a vast array of vector species. Therefore, each species has to be individually evaluated regarding how specialized or generalized its pollination system actually is.

So the question becomes, why do some plant species adopt more inclusive guilds of potential pollinators that include species of dissimilar sizes and behaviors representing different taxonomic groups? When this occurs, we refer to the plant as having adopted a generalist pollination strategy (see Heithaus 1974; Waser et al. 1996; Gomez and Zamora 2006; Olesen et al. 2007; Ollerton et al. 2007 for a more complete overview of the generalist strategy).

From the perspective of an annual plant, a generalist pollination strategy tends to increase the likelihood of at least some successful fruit/seed set in fluctuating environments that are the norm in the variable southern California Mediterranean climate (Waser et al. 1996; Gomez and Zamora 2006). However, there may be genetic consequences related to the different sets of insect vectors and their behavior, ranging from visits of many flowers on a single plant before moving to the next plant (favoring selfing), to moving quickly among flowers on separate plants (favoring outcrossing) (Stebbins 1950; Schmitt 1983). In our study, rainfall varied considerably between the times of the study at the Ahmanson and Newhall Ranch sites (2001 and 2004 respectively) and resulted in many fewer SFVS plants being produced at both sites during the 2004 season than had been produced in 2001. Fewer plants mean fewer resources are available to attract and hold the services of potential pollinators, especially those with high energy requirements like the European honey bee (Johnson and Hubbell 1975; Schaffer et al. 1979; Sih and Baltus 1987; Jennersen and Nilsson 1993; Conner and Neumeier 1995). However, a decrease in resources should not be as important to potential pollinators with minimal energetic requirements such as ants and other small-bodied pollinators.

In our study, 2001 was a good year and produced sufficient SFVS plants that the bloom even attracted the European honey bee, *Apis mellifera*, which was one of the top five visitors to the plants that season (Jones et al. 2002). However, the 2004 year was much drier and produced many fewer SFVS plants at both sites (Ahmanson and Newhall Ranches) and resulted in no honey bees being attracted to these plants, even though they were observed visiting other taxa in the vicinity (Jones et al. 2004). During both seasons, ants were common visitors to the SFVS plants. As a result of the way they forage, ants would tend to facilitate selfing more frequently than outcrossing (Jones et al. 2002, 2004; unpublished data). In contrast, honey bee behavior on these flowers would tend to increase the probability of outcrossing over selfing. Although honey bees collected both nectar and pollen when visiting the SFVS flowers, the minimal nectar rewards produced per flower, forced them to visit many flowers to achieve a full nectar crop prior to returning to the hive.

An intriguing aspect to consider is how such annual differences in pollinators might affect the genetic structure of the offspring in any given season. One would expect that the progeny produced during drier years would reflect more selfing, whereas that produced in wetter years would reflect more outcrossing. It would be quite interesting to collect seed produced under such environmental conditions and examine the genetic variation of progeny produced to determine if pollinators have significant effects on the genetic structure of the progeny produced during such divergent rainfall years (Barrett 2002).

Local Invertebrate Community in the Coastal Sage Scrub Plant Community and Potential Pollinators for the SFVS

The insect community at the Newhall Ranch was quite diverse and both sampling methods captured a number of infrequent species as evidenced by the high percentage (~50%) of species represented by only a single specimen (singletons). Given this and the fact that the species accumulation curves did not reach an upper asymptote, it is very likely that we have underestimated the insect diversity in this community. However, these results are not unlike other studies of arthropod communities in coastal sage scrub (CSS). Burger et al. (2003) found that approximately 51% of their 169 morphospecies were represented by a single specimen. Their results and ours suggest that the terrestrial arthropod community in the surrounding community is very diverse and that adequately sampling the terrestrial arthropod diversity will require a much greater effort than that represented in this study.

We found that 14 of 101 insect morphospecies were captured on the flowers of the SFVS and might be potential pollinators. Of these 14 species, 10 carried grains of SFVS pollen. Interestingly, our sample of potential pollinators contained 8 singletons, which also suggests that there is a substantial number of species with very low abundance in this community and, again suggests that we have probably underestimated the insect diversity in this community. Regardless of these issues, it is clear that the most abundant orders of insects in our sample (e.g., Hymenoptera, Coleoptera) also represent the largest number of potential pollinators.

Seed Set and Pollinator Limitation

The effectiveness of the SFVS visitors as pollinators is demonstrated, at least partially, by the high seed set (50–60%) registered in both sets of controls associated with the exclusion experiments completed at the Ahmanson Ranch study site. Additionally, the data suggest that the contribution of ants and flying insects to seed set is equivalent to that of aerial visitors alone. This would indicate that ants are not normally required for full seed set and supports the idea that this species has adopted a generalist pollination strategy (Waser et al. 1996; Gomez and Zamora 2006). However, ants may be important pollinators when other vectors are scarce (Jones, et al., unpublished data) The actual pollinating species may depend primarily upon vector availability, the diversity of which varies with seasonal and annual environmental fluctuations. In any case, pollinator limitation would appear not to be a problem for the SFVS.

Pollinator Constancy

Harper (1979) has noted that most rare plant taxa rely on insect pollination and that survival of many rare plants depends on the maintenance of sufficient pollinator populations. As defined here, constancy is the condition that exists when a floral visitor frequents only a single species on a given foraging bout. Many pollinators such as honeybees, bumblebees and lepidopterans have demonstrated constancy to specific species (Free 1963; Lewis 1989; Goulson et al. 1997). Such flower constancy increases the likelihood of a plant receiving pollen from a member of the same species and, in turn, increases the likelihood of successful fertilization. This also generally decreases the flower handling time for the pollinator (Waser 1986; Chittka et al. 1999). In addition, when pollinators visit a single species they are less likely to transfer a pollen grain of another species that could possibly clog the stigma with incompatible pollen (Waser 1986; Chittka et al. 1999). Frequently rare species exhibit reduced seed set (Baskin and Baskin 1998), one possible symptom of low constancy. However, seed set and constancy are both high in the SFVS.

Constancy, as determined by captured specimens from both the Ahmanson and Newhall Ranches (details for the latter are given in table 4 in Jones et al. 2004), was high among most of the floral visitors. The significant number of visitors, both terrestrial and aerial, demonstrating constancy to the SFVS may also be reinforced by the patchy distribution pattern of this taxon, which facilitates both nectar collection and constancy (Chittka et al. 1999).

Although we examined a relatively small sample of ants captured on SFVS flowers at the Ahmanson Ranch, those that were had pollen loads that were 98% specific to the flowers of the SFVS, indicating that these ant species were purposefully visiting these plants, using them as a food source, and in the process picking up pollen and probably facilitating the successful reproduction of the SFVS (Jones et al. 2002).

Nectar Availability

Nectar production has an energetic cost for plants. Plants of arid environments with profuse flower production per plant and subjected to fluctuating rainfall from year to year are likely to produce smaller individual flowers and less nectar per flower when under stress. Consequently, their normal nectar production per flower may very well be relatively small due to this evolutionary constraint (Southwick 1984; De la Barrera and Nobel 2004). The SFVS occupies a seasonally dry habitat that varies considerably in the amount of rainfall received prior to and during the growing season of the plant. Quite likely as a result of such constraints, the nectar production per flower in the SFVS is minimal.

In such cases there is still a possibility that through rapid visits to a large number of flowers pollinators could be able to collect sufficient nectar to satisfy their energetic needs (especially taxa with higher energetic demands, Spira 1980). In comparison to the average nectar per flower found in bee flowers (Cruden et al. 1983), the low nectar production per flower observed in the SFVS forces larger bodied floral visitors (like honey bees) to visit many flowers during a single foraging bout, helping to ensure the pollination of many flowers and, perhaps, facilitating increased outcrossing among plants in the population (Proctor et al. 1996).

It is interesting to note that diurnal nectar production was highest during the early afternoon and remained fairly constant throughout the remainder of the day. Floral visitation was also highest during this period, particularly among the ants, which are smaller bodied potential pollinators that have smaller energetic requirements per individual (Peters 1983; Degen et al. 1986).

Breeding System—Selfing

Our data from the bagging experiments completed at the Ahmanson Ranch study site indicate that the SFVS is at least partially self-fertile. In fact, nearly 30% of the flowers set fruit with viable seeds in our controlled experiments where the plants were bagged preventing any pollination vectors from having access to the flowers; thus, these flowers set fruit without the services of a vector. However, our data also indicate that more flowers set fruit when the flowers are exposed to potential pollination vectors. It would appear that at least some of this fruit set is due to cross pollination suggesting that the SFVS can probably set fruit by selfing when pollinators are limiting or when pollinators are small and tend to frequent many flowers on the same plant (ants), as well as, by outcrossing when pollinators are abundant or when larger pollinators such as honey bees are among the floral visitors.

Stebbins (1957) indicated that geographically restricted plants, such as the SFVS, are likely to be self-compatible. He postulated that in species whose populations fluctuate frequently, selection would favor self-compatibility during times of smaller populations. He also suggested that self-fertilization is common in annual plants of California and other Mediterranean regions due to dramatic climate variability. During particularly dry years, conditions favorable for cross-pollination may be absent or only present for a short time. Furthermore, Hagerup (1932) suggested that dry climates lead to lower populations of pollinators and Roubik (2001) has shown annual variability in pollinator populations.

Karron (1991) and Barrett (2002) have also noted that rare plant taxa may be more likely to be self-compatible than more widespread species. Numerous rare plant species have been shown to be self-fertile (Kunin and Shmida 1997; Bosch et al. 1998; Anderson et al. 2001). These self-pollinating flowers generally have smaller, less showy flowers (Proctor et al. 1996; Barrett 2002). Such small flower size and short relative distance from anther to stigma are also often associated with self-compatibility (Kunin and Shmida 1997; Anderson et al. 2001). The SFVS demonstrates these characteristics.

Situations in which some fraction of the fruit is set by selfing and some fraction is set by outcrossing creates a mixed mating strategy (Vogler and Kalisz 2001). Such a strategy appears to be present in plants found in seasonally variable habitats with unpredictable rainfall regimes, resulting in large variations in plant population sizes and unpredictable pollination vector populations. Under these conditions, a mixed mating strategy seems to provide some assurance of reproductive output each and every year (Barrett 2002, 2003). A more thorough discussion of the potential roles of ants versus honey bees in facilitating selfing or outcrossing and a discussion of the potential importance of each to the continued survival of the SFVS will be presented in a separate paper (Jones et al. unpublished data).

Seed Germination

Plants require more than successful pollination and fertilization to complete sexual reproduction. First, the seeds produced must also be viable. Secondly, many species have complex germination patterns (Bewley and Black 1994) that may contribute to differential survival and recruitment (Burdon et al. 1983), an important consideration in the biology of rare species. Therefore, an examination of the germination potential of any seeds produced is necessary in order to form an accurate picture of the reproductive capacity of a particular species.

In general, SFVS seeds seem to germinate easily, without the need for any special treatment. Even the seeds that did not germinate may remain viable and might actually represent seeds that exhibit delayed germination and become part of a seed bank (Baskin and Baskin 1998). Although SFVS seeds that were subjected to special treatments seemed to germinate at a lower rate than control seeds, this may be due simply to the short timeline of these experiments. Stratification, in particular, appeared to slow the germination process but this may result from the slowing effects of lower temperatures *per se* on physiological processes, rather than on special seed dormancy requirements. Obviously, this aspect of the reproductive process requires further study.

An accompanying study of possible fire-related germination cues, such as heat shock, smoke, and charred wood showed that none of these treatments significantly stimulated germination in the SFVS (Sandquist 2003).

The general ease of germination allows for the rapid establishment of SFVS populations in open spaces, much like a weedy strategist (Baskin and Baskin 1998), and supports the establishment of the dense patches that provide the floral display and nectar resources required to attract flying pollen vectors. Clearly, maintenance of these dense patches in the face of drought, disturbance and alien species should be a matter of concern for managers.

Conservation Concerns—Effects of Population Size Variability

Low population sizes, resulting in decreased floral display and nectar resources, would be expected to lead to decreases in the number of flying visitors. Our data indicate that during harsh, dry, growing seasons, as was the case for our Newhall Ranch study, the SFVS may survive by producing a significant number of progeny via selfing without a vector. A significant decrease in the number of floral visitors or the production of a significant number of progeny via selfing without a vector would have important genetic implications in terms of interpopulation gene flow (Barrett 2002). Certainly, an additional study that should be undertaken is a detailed analysis of the population genetics of this species throughout its extant range in order to determine its genetic health and to establish management strategies to maintain or enhance that health.

Summary

The reproductive biology of the SFVS, at least in the aspects studied here, appears to be characterized by great flexibility. No special treatment was required for seed germination, allowing for the rapid establishment of the dense SFVS patches observed in the field. Pollination interactions involved a substantial variety of insects, both terrestrial and aerial, and included a mixed mating system characterized by being able to set fruit without the need of a pollination vector. However, far more fruit were set when the flowers were exposed to potential pollination vectors. Five species at the Ahmanson Ranch were responsible for 75% of the total visits to SFVS flowers: *Apis mellifera*; two species of native ants, *Dorymyrmex insanus* and *Solenopsis xylonii*; and two species of beetles, *Zabrotes* sp. and *Emmenotarsis quadricollis*. The small size of the latter four native species (all under 5 mm in length) allows easy entry into the SFVS flowers, whereas the larger, introduced, *Apis mellifera* accesses the nectar rewards with its long proboscis. At the Newhall Ranch, by far the most common insect captured on the flowers of the SFVS (17 of 43 or 39.5%) was the small red ant, *Forelius mccooki*.

Size and mobility differences among these six prominent visitors may have implications for their respective roles in the SFVS pollen flow. Flight distance and, therefore, pollen dispersal range is much greater for *Apis mellifera* than for the five native species. The five native species tend to visit flowers on the same plant (the SFVS proved to be a facultative selfer) or on nearby neighbors. It would seem that *Apis mellifera* would foster longer distance pollen dispersal than the other four species and would have a greater likelihood of facilitating outcrossing. Native bees may normally play this role but few were observed during this study. Therefore, the role of the smaller species might be one of facilitating reproductive success through within-plant or within-patch pollination, whereas the larger, more mobile pollinators, like *Apis mellifera*, should provide the inter-patch or inter-subpopulation pollen flow important for the maintenance of the SFVS genetic diversity. The presence of both guilds of pollinators should facilitate overall reproductive success. Clearly, this generalized pollination strategy would be highly advantageous in an environment with large spatiotemporal variability such as that found in the southern California climate zone, where seasonal and annual variation in pollinator assemblages appears to be substantial.

Although visits to flowers of the SFVS do not necessarily correspond to successful pollination events, because of the diversity and frequency of the observed visitors and the fact that the data were only taken on visitors that were actually visiting the stamens and/or came into contact with the stigmatic surfaces, we conclude that the SFVS is not likely to be pollinator limited. Further, it is neither limited by lack of seed production nor seed germination. We conclude with the suggestion that this species may be rare due to the destruction of suitable habitat.

Acknowledgments

The authors thank Senta Breden, Mina deLeest, Kelly Garron, Dawn Hendricks, Fern Hoffman, Katie Levensailor, Jamie Miner, Greg Pongetti, Nelida Rojas, Romeo Sison, and Matthew Weekes for field assistance, the staffs at the Ahmanson and Newhall Ranches, Dudek and Associates, Inc., Sapphos Environmental, Inc., and Lenora O. Kirby of the Las Virgenes Institute for their assistance, as well as Roy Snelling, Charles L. Bellamy, Eric Fisher and Steve Gaimari for arthropod identifications. Contract grant support from Newhall Land and Farming Corp., Newhall, California, via Dudek and Associates, Inc., Encinitas, California and from Sapphos Environmental Inc., Pasadena, California is gratefully acknowledged.

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